

Peatland bryophyte responses to increased light from black spruce removal

Leonard, Rhoswen; Kettridge, Nicholas; Krause, Stefan; Devito, Kevin J.; Granath, Gustaf ; Petrone, Richard; Mendoza, Carl

DOI:
[10.1002/eco.1804](https://doi.org/10.1002/eco.1804)

License:
Creative Commons: Attribution (CC BY)

Document Version
Publisher's PDF, also known as Version of record

Citation for published version (Harvard):
Leonard, R, Kettridge, N, Krause, S, Devito, KJ, Granath, G, Petrone, R & Mendoza, C 2017, 'Peatland bryophyte responses to increased light from black spruce removal', *Ecohydrology*, vol. 10, no. 1, e1804. <https://doi.org/10.1002/eco.1804>

[Link to publication on Research at Birmingham portal](#)

General rights

Unless a licence is specified above, all rights (including copyright and moral rights) in this document are retained by the authors and/or the copyright holders. The express permission of the copyright holder must be obtained for any use of this material other than for purposes permitted by law.

- Users may freely distribute the URL that is used to identify this publication.
- Users may download and/or print one copy of the publication from the University of Birmingham research portal for the purpose of private study or non-commercial research.
- User may use extracts from the document in line with the concept of 'fair dealing' under the Copyright, Designs and Patents Act 1988 (?)
- Users may not further distribute the material nor use it for the purposes of commercial gain.

Where a licence is displayed above, please note the terms and conditions of the licence govern your use of this document.

When citing, please reference the published version.

Take down policy

While the University of Birmingham exercises care and attention in making items available there are rare occasions when an item has been uploaded in error or has been deemed to be commercially or otherwise sensitive.

If you believe that this is the case for this document, please contact UBIRA@lists.bham.ac.uk providing details and we will remove access to the work immediately and investigate.

ECO LETTER

Peatland bryophyte responses to increased light from black spruce removal

R. Leonard¹ | N. Kettridge¹ | S. Krause¹ | K.J. Devito² | G. Granath³  | R. Petrone⁴ | C. Mendoza⁵ | J.M. Waddington⁶

¹School of Geography, Earth and Environmental Sciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK

²Department of Biological Sciences, University of Alberta, Edmonton T6G 2E9AB, Canada

³Department of Ecology, Swedish University of Agricultural Sciences, Box 704475007 Uppsala, Sweden

⁴Department of Geography and Environmental Management, University of Waterloo, Waterloo, ON N2L 3G1, Canada

⁵Department of Earth and Atmospheric Science, University of Alberta, Edmonton, AB T6G 2E3, Canada

⁶School of Geography and Earth Sciences, McMaster University, Hamilton, ON L8S 4K1, Canada

Correspondence

Rhoswen Leonard, School of Geography, Earth and Environmental Sciences, University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK.

Email: rml343@bham.ac.uk

Funding information

Natural Sciences and Engineering Research Council, Grant/Award Number: CRDPJ477235-14

Abstract

The ecohydrological impact of tree-canopy removal on moss and peat, which provide a principal carbon store, is just starting to be understood. Different mosses have contrasting contributions to carbon and water fluxes (e.g., *Sphagnum fuscum*, *Pleurozium schreberi*) and are strongly influenced by tree-canopy cover. Changes in tree-canopy cover may therefore lead to long-term shifts in species composition and associated ecohydrological function. However, the medium-term response to such disturbance, the associated lag in this transition to a new ecohydrological and biogeochemical regime, is not understood in detail. We investigate this medium-term (4 years) ecohydrological, biogeochemical, and species compositional response to tree-canopy removal using a randomized plot design within a northern peatland. This is the only study to test for the influence of increased light alone. We demonstrate that changes in treatment plots 4 years after tree-canopy removal were not significant. Notably, *P. schreberi* and *S. fuscum* remained within their respective plots post treatment, and there was no significant difference in plot resistance to evapotranspiration or carbon exchange. Results show that tree-canopy removal alone has little impact on bryophyte ecohydrology in the short or medium-term. This resistance to disturbance contrasts strongly with short-term changes observed within mineral soils, suggesting that concurrent shifts in the large scale hydrology induced within such disturbances are necessary to cause rapid ecohydrological transitions. Understanding this lagged response is critical to determine the strength of medium to long-term negative ecohydrological feedbacks within peatlands in addition to carbon and water fluxes on a decadal timescale in response to disturbance.

KEYWORDS

boreal, feathermoss, peat, *Sphagnum*, tree-canopy disturbance

1 | INTRODUCTION

Boreal forests occupy approximately 10% of the earth's vegetated surface (McGuire, Melillo, Kicklighter, & Joyce, 1995), of which, peatlands are a dominant feature. These northern peatlands are estimated to be one of the world's largest carbon stores (Yu, 2012). Despite this, northern forested peatlands are subject to widespread tree-canopy disturbances. Linear tree clearance from seismic lines exceeds 1.5 Mkm in Alberta, Canada, alone (Timoney & Lee, 2001). This equates to a 19-Mha disturbance assuming a 60-m edge effect.

Thinning of spruce stands is used as a fire control method. In addition, insect infestations have the potential to act as a significant future disturbance with increases in the frequency and severity of fire and drought projected to reduce tree-canopy resistance to insects and disease (Raffa et al., 2008). Such disturbances not only remove the tree-canopy but also impact the ecohydrological function of the moss and peat (Kettridge et al., 2013), which provide the principal carbon store within these carbon rich ecosystems.

Mosses play an integral role in ecosystem functioning with their ability to equal or exceed tree-canopy productivity within northern

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2016 The Authors Ecohydrology Published by John Wiley & Sons Ltd

forested peatlands (Bisbee, Gower, Norman, & Nordheim, 2001) and contribute up to 69% of total ecosystem evapotranspiration (Bond-Lamberty, Gower, Amiro, & Ewers, 2011). Typically, feather mosses (e.g., *Pleurozium schreberi*) are associated with a high black spruce stand density and *Sphagnum* carpets are more typical of open tree-canopy peatlands. A combination of these floor cover types exist on peatlands with low stand density. Since tree cover controls the moss layer environment (e.g., temperature and radiation), its loss or thinning results in different ground layer species compositions as a result of competition and extinction-colonization dynamics. Feather moss groundcover percentage is negatively related to tree-canopy transmittance of photosynthetically active radiation (PAR), when *Sphagnum* is present while percentage ground cover of *Sphagnum* is positively related to tree-canopy PAR transmittance (Bisbee et al., 2001). This suggests that thinning of tree canopies will increase *Sphagnum* cover. Carbon and water fluxes would alter as a result because *Sphagnum fuscum* is three times more productive than *P. schreberi* (Bisbee et al., 2001) and evaporates much more due to its enhanced water transport abilities (McCarter & Price, 2014).

Short-term studies within mineral soils suggest that *S. fuscum* cover increases in the first years after tree-canopy removal (Fenton & Bergeron, 2007) and *P. schreberi* shows complete absence after 1 year (Shields, Webster, & Glime, 2007) or significant decreases in cover after 4 years (Fenton, Frego, & Sims, 2003). Despite the extent of tree-canopy disturbance within carbon rich forested peatlands, and their strong control over water and carbon fluxes, the medium-term response of moss species composition that characterizes the transitional periods of lagged responses and their associated carbon and water fluxes, remains largely unstudied. It may be argued that transitional phases dominate peatland composition and function, particularly in boreal Alberta. The cycling of disturbances such as fire, thinning, clear cutting, and seismic line creation is continuous in this region, resulting in a patchwork of continually responding ecosystems, yet work at the response/transitional phase (medium-term) timescale is rarely considered. Findings of short-term studies may change in the medium-term because the disturbance/treatment response processes may take longer than their study period. For example, a decline in *S. fuscum* 2 years after tree-canopy removal is suggested to have been a result of physiological shock due to exposure to new conditions (Fenton & Bergeron, 2007) and is likely to recover (Clymo & Duckett, 1986). In addition to lack of medium-term studies, we are not aware of any that report or demonstrate minimal changes in water-table depth and/or the impact of machinery. These are common confounding factors in large-scale timber clearances where most tree-canopy removal studies have taken place.

We target these key knowledge gaps by investigating the ecohydrological, biogeochemical, and compositional response of two key northern bryophytes to tree-canopy removal. The experiment is uniquely conducted with before and after treatment (tree-canopy removal) plots in a black spruce peatland, with no additional factors (e.g., disturbance related changes in water levels and surface micro topography), allowing unequivocal evaluation of medium-term moss response to changes in light conditions alone. The isolation of light as a process that likely induces changes to the influential moss layer will allow more robust and flexible modeling and predictions of peatland ecohydrological functioning to various disturbances

including, tree removal, insect infestations, and any other light increasing disturbances.

2 | STUDY SITE

Experiments were conducted on a poor fen in central Alberta, Canada (55.81°N, 115.11°W). The depth of peat is ≥ 3 m and the hydrological regime is such that it is part of a larger flow-through system within the landscape, resulting in a stable water table. Total annual precipitation for (for the study period) 2010, 2011, 2012, 2013, 2014, 2015 was 282, 489, 497, 523, 376 and 387 mm, respectively. The study site is characterized by a tree cover of *Picea mariana* with a basal area and average height of $11 \text{ m}^2 \text{ ha}^{-1}$ and 2.3 m respectively. Tree basal areas for northern Albertan peatlands range from 0.3 to $47.3 \text{ m}^2 \text{ ha}^{-1}$ for peatlands that are 21 to 100 years since fire, respectively (Wieder et al., 2009). Ground layer vegetation is composed of *S. fuscum*, *Sphagnum angustifolium*, and *P. schreberi* with vascular species that include *Rhododendron groenlandicum*, *Rubus chamaemorus*, *Chamaedaphne calyculata*, *Maianthemum trifolia*, *Vaccinium oxycoccus*, and *Vaccinium vitis-idea*.

3 | METHODS

In May, 2010, 20 polyvinyl chloride collars (inside diameter of 0.17 m, length 0.10 m) were installed in the ground based on the species present ($10 \times S. fuscum$ and $10 \times P. schreberi$, each with 100% cover). No significant differences in sky view factor between the proposed control (0.60 ± 0.08) and treatment (0.65 ± 0.09) plots ($p > 0.05$, $t = -1.58$) or between the *S. fuscum* (0.60 ± 0.06) and *P. schreberi* (0.64 ± 0.11) plots ($p > 0.05$, $t = -1.16$) were found. On June 17, 2010, trees around five randomly selected *S. fuscum* collars and five randomly selected *P. schreberi* collars were cut by hand to increase sky view factor at the collar. Trees within a 5 m radius that influence the available light at the plot were removed, which significantly increased the sky view factor in the treatment plots (0.85 ± 0.03) relative to the control plots (0.60 ± 0.08) ($p < 0.001$, $t = 9.7$). Relative humidity (%) did not differ significantly between treatment and control plots ($p = 0.91$, $t = -0.11$) or between species ($p = 0.22$, $t = 1.3$). Air temperature did not differ significantly between treatment and control plots ($W = 42$, $p = 0.58$) or between species ($W = 62$, $p = 0.39$) either. Between June and August 2010, soil moisture and surface resistance to evapotranspiration were measured 15 times within each collar. Between July and August, 2014, measurements of species composition, and five repeat measurements of surface resistance (r_s), CO_2 exchange (net primary productivity, respiration, net ecosystem exchange), and soil moisture were undertaken within each collar. Moss stress (chlorophyll fluorescence) was measured in all plots at intervals between 7 a.m. and 6 p.m. in 2015. All measurement dates were randomly selected between May and August of each respective year, provided that there was no precipitation on the day of measurement.

Bryophyte species cover was estimated as a percentage for each collar. Moisture measurements were taken at 0.06 m depth (repeats of $n = 5$ were taken during 2010 and 2014). Resistance to evapotranspiration and CO_2 exchange were measured using a closed chamber system in accordance with McLeod, Daniel, Faulkner, and Murison

(2004). A cylindrical clear plexiglass chamber (volume of 12.6 L) was placed over the collar for 2 min and the air inside mixed continuously using a small fan. Changes in the humidity and CO₂ concentration within the chamber were measured every 1.6 s using a PP systems EGM4 infra-red gas analyser. A dark (opaque) chamber with the same dimensions was used to measure respiration (respiration assumed equal to dark chamber CO₂ flux) by the same method as described for resistance to evapotranspiration. Light chamber measurements were immediately followed by dark chamber measurements between 9 a.m. and 5 p.m. Temperature measurements were taken at 0.02 m below the bryophyte surface. Evapotranspiration rate (ET) was calculated from the slope of the linear change in vapor density (Stannard, 1988) during the first 35 s of measurement because changes in vapor density reduce significantly after the first minute (also reported by Kettridge et al. (2013)). The surface resistance to evaporation (r_s) is equal to

$$r_s = \frac{\rho_{vs}^* - \rho_{va}}{ET} - r_a, \quad (1)$$

where ρ_{vs} and ρ_{va} are the saturation vapor density of the peat surface and the vapor density of the air within the chamber, respectively and r_a is the aerodynamic resistance within the chamber during a measurement (calculated by placing the chamber over a water bath at room temperature ($r_s = 0$) and calculating evaporation accordingly using the same setup and duration as the field method).

3.1 | CO₂ flux

Net ecosystem exchange (NEE) was calculated from (Shaver, Street, Rastetter, Van Wijk, & Williams, 2007),

$$NEE = \frac{\rho V dC}{A dt}, \quad (2)$$

where ρ is air density (mol/m³), V is the volume of the chamber plus base (m³), A is the projected horizontal surface area of the chamber (m²), and dC/dt is the rate of change in CO₂ concentration within the plexiglass chamber (μmol mol⁻¹ s⁻¹). Ecosystem respiration (RE;

μmol m⁻² s⁻¹) was calculated in accordance with Equation 2 but with dC/dt determined within a dark (opaque) chamber. Gross ecosystem productivity (GEP) is equal to NEE-RE, where a negative value indicates carbon uptake and a positive value indicates carbon release.

3.2 | Chlorophyll fluorescence measurements

Maximum quantum yield of photosystem II (F_v/F_m) was used to assess plant stress in response to tree-canopy removal due to its sensitivity as an indicator of plant photosynthetic performance (Maxwell & Johnson, 2000). An OS30p handheld chlorophyll fluorometer was used to measure F_v/F_m after 20 min of dark adaptation (Maxwell & Johnson, 2000) of mosses in each treatment. The theoretical maximum of F_v/F_m is between 0.78 and 0.89 (Adams & Demmig-Adams, 2004). Individual species will have different optimal values when un-stressed. Lower than optimal values indicate a lowered photosynthetic capacity (or stress); normally, this is water stress for bryophytes (Maxwell & Johnson, 2000). Chlorophyll fluorescence measurements were taken from all plots at regular intervals between 6 a.m. and 6 p.m. on July 17, 2015 to compare between control and treatment diurnal patterns.

All statistical analyses were conducted in R. A Wilcoxon rank-sum test was used to determine differences between percentage cover of bryophyte abundance between control and treatment plots (2014), daily average F_v/F_m treatment, and control plots of each species (2015). Repeat measures of moisture, GEP, and r_s from each collar were averaged. An ANOVA comparing species, year (where appropriate: moisture and r_s) and treatment were undertaken.

4 | RESULTS

4.1 | Species cover

Plots in 2010 were selected to include 100% cover of the respective species. *S. fuscum* and *P. schreberi* were still present in the relevant treatment and control plots in 2014 (Table 1). No significant difference was observed in either species abundance as a result of treatment. All *S. fuscum* plots contained 100% *S. fuscum* cover in treatment and

TABLE 1 Species cover percentages for all plots (5 of each species) in 2010 and 2014

			Control 2010	Open 2010	Control 2014	Open 2014
Pleurozium schreberi plots	<i>P. schreberi</i>	Mean	100.0	100.0	99.0	60.4
		SE ±	0.0	0.0	2.0	17.1
		median	100.0	100.0	100.0	75.0
		range	0.0	0.0	5.0	98.0
	Bare ground	Mean	—	—	0.0	21.4
		SE±	—	—	0.0	16.5
		median	—	—	0.0	2.0
		range	—	—	0.0	95.0
	<i>Aulacomnium palustre</i>	Mean	—	—	0.0	4.6
		SE±	—	—	0.0	3.5
		median	—	—	0.0	0.0
		range	—	—	0.0	20.0
	<i>Polytrichum strictum</i>	Mean	—	—	0.6	1.0
		SE±	—	—	0.5	0.9
		median	—	—	0.0	0.0
		range	—	—	3.0	5.0
<i>Sphagnum fuscum</i> plots	<i>S. fuscum</i>	Mean	100.0	100.0	100.0	100.0
		SE±	0.0	0.0	0.0	0.0
		median	100.0	100.0	100.0	100.0
		range	0.0	0.0	0.0	0.0

control plots. Although *P. schreberi* showed a decline (mean of percentage cover in control = 99% ($SE \pm 0.89$, median = 100, range = 95 to 100), mean of percentage cover in treatment = 60% ($SE \pm 17.1$, median = 75, range = 2 to 100), this was not significant ($p = 0.06$, $n = 5$). *P. schreberi* remained present in all 10 collars in 2014.

4.2 | Gross ecosystem productivity, surface resistance and moisture

In 2014, gross ecosystem productivity did not differ significantly between treatment types but did show significant differences with species (Table 2 and Figure 1) with *S. fuscum* (mean: -6 , ± 0.6 SE) more productive than *P. schreberi* (mean: -12 , ± 0.9 SE). Surface resistance was significantly different between species (i.e., r_s greater in *P. schreberi* plots: Figure 2) but did not show a treatment effect (Table 2). Moisture in the top 0.06 m also did not differ significantly with treatment but did show a significant species and year effect (Table 2 & Figure 3).

4.3 | Chlorophyll fluorescence

In 2015, both mean *P. schreberi* and *S. fuscum* F_v/F_m in the control collars remained near optimal throughout the day, only reaching a low of 0.66 for *S. fuscum*. The *S. fuscum* treatment fell as low as 0.63. The *P. schreberi* treatment plots on the other hand showed a drop in mean F_v/F_m later in the day to 0.46 at 4 p.m (Figure 4). Differences between treatment and control *S. fuscum* F_v/F_m were not significant ($p = 0.69$, $n = 5$). However, the treatment did cause significant reductions in *P. schreberi* F_v/F_m values ($p = .0079$, $n = 5$).

5 | DISCUSSION

5.1 | Species response to disturbance

Pleurozium schreberi is negatively correlated to the tree-canopy PAR transmittance when *Sphagnum* is present and is typically found under dense tree covers (Bisbee et al., 2001). *Sphagnum* is positively correlated with tree-canopy PAR transmittance and associated with open tree-canopy areas (Bisbee et al., 2001). It is therefore likely that long-term shifts toward an *S. fuscum* dominated system will occur in response to tree-canopy removal. Despite this, tree-canopy removal

alone did not cause any significant changes in species compositions in the medium-term. *P. schreberi* was present in all treatment collars 4 years after tree-canopy removal and showed no significant decrease in cover. We suggest here that the tree-canopy PAR transmittance, substrate type, depth, and its associated hydrology not only control the species distribution (Bisbee et al., 2001) but also modify the rate of this transition in response to tree-canopy removal.

Decline in *P. schreberi* has been attributed to increased evaporation stress. If tree-canopy cover is not adequate to prevent evaporation stress, feather mosses dry out and die because they are nearly independent of the substrates' water supply (Johnson, 1981). Thus, evaporative stress will provide the likely driver for the expected long-term transition from *P. schreberi* to *S. fuscum* after tree-canopy removal. *P. schreberi* treatment plots exhibit less optimal F_v/F_m values compared to control plots, resulting in reduced carbon accumulation which slowly reduces their competitive strength and groundcover. Further work is required to determine how the duration and intensity in *P. schreberi* stress varies on a diurnal cycle, its association with tree-canopy removal, its link with evaporative demand and near-surface moisture/tension. However, this evaporative stress is the probable cause of the observed decline of *P. schreberi* abundance and long-term shift to a *Sphagnum* dominated system. We observed that if increased evaporative stress associated with increased solar radiation is acting alone, the resulting shift in species occurs much slower, with no significant changes found within 4 years, suggesting the response is lagged. This lagged response left subcanopy species outside of their niche environment, in this experiment, for a period of greater than 4 years.

Despite the slower response observed in this study, Shields et al. (2007) and Fenton et al. (2003) observed a complete loss of *P. schreberi* within mineral soils 1 year after tree-canopy removal and a significant decrease after 4 years, respectively. This significant and rapid decrease/absence of *P. schreberi* in response to tree-canopy removal in short-term, mineral soil studies may be a result of changes in near-surface moisture saturation levels. A change in the moisture regime as a side effect of tree-canopy removal may be due to a change in any combination of the following: substrate depth, substrate storage, transpiration rates (lack of, after disturbance), disturbance size, and compaction. If the balance between the water storage available and reduction in evapotranspiration through tree removal results in a water table rise to a level unfavourable for *P. schreberi*, changes in species compositions may occur at a faster rate. Tree removal can result in a

TABLE 2 ANOVA results of comparisons between species, treatment and year for moisture, surface resistance and gross ecosystem productivity

	Moisture (Mv)		Gross ecosystem productivity ($\text{gC m}^{-2} \text{s}^{-1}$)		Surface resistance (s/m)	
	F value (1/16)	p value	F value (1/16)	p value	F value (1/16)	p value
(Intercept)	201.70	<.0001	207.73	<.0001	90.57	<.0001
Species	22.52	.0002*	22.85	.0002*	21.21	.0003*
Treatment	0.16	.7	0.13	.72	0.03	.87
Year	21.77	.0003*			0.40	.53
Species:Treatment	0.58	.46	0.62	.44	0.07	.79
Species:Year	1.05	.32			0.33	.58
Treatment:Year	0.16	.7			3.54	.08
Species:Treatment:Year	0.02	.89			1.72	.21

Note. Asterisk (*) = significant.

water table rise (due to lack of transpiration; Pothier, Prévost, & Auger, 2003), which causes negative effects in feather moss (Busby, Bliss, & Hamilton, 1978) in as little as 4 months (Birse, 2016). However, near-surface moisture conditions did not change significantly within our study. It is also unlikely that water levels changed significantly, due to the small scale of the disturbance (and low predisturbance transpiration rate) and the fact that the system has groundwater through flow. This ground water through flow limits large water level fluctuation that would adversely affect the studied mosses. The small scale nature of the experiment on a large groundwater fed fen facilitates the minimization of water level changes as a confounding effect (which is supported by soil moisture results; Figure 3). Further, such a rapid transition may be exacerbated by the tree clearance method employed. For instance, machinery used for harvesting can cause variable changes in forest floor depth by substrate compaction (Mariani, Chang, & Kabzems, 2006). Trees were cut by hand in this study, therefore, eliminating the influence of such disturbance. The lack of observed ecohydrological changes may have also been due to low predisturbance tree densities, resulting in a less extreme increase in light than in comparative studies (Shields et al., 2007; Fenton et al., 2003). However, the sky view factor was significantly reduced in the treatment plots. At a sky view factor of 0.85, both species could maintain their presence and ecohydrological functioning. Further work is

required to assess whether the predisturbance tree density or sky view factor has an impact on species presence and ecohydrological function. However, given the high sky view factor values for treatment plots, this study highlights that light alone is not enough to rapidly change species composition.

Sphagnum fuscum percentage cover did not change between control and treatment collars. This was expected because *S. fuscum* usually grows in areas with a less dense tree cover (Bisbee et al., 2001). *S. fuscum* decline in literature has been attributed to a physiological shock in response to increased light levels (Fenton & Bergeron, 2007). This may have occurred in the short-term after which the *S. fuscum* subsequently recovered (Clymo & Duckett, 1986). For example, Locky and Bayley (2007) found a decline in *Sphagnum* cover 1 to 4 years after tree-canopy removal but a subsequent increase after 9 to 12 years.

5.2 | Hydrological and biogeochemical response

Differences in *P. schreberi* GEP and r_s between treatment and control collars were not significant in this study (Figures 1 and 2). The lack of connectivity with a water supply means that *P. schreberi* can only evaporate until the water available (from precipitation (Busby et al., 1978), dew and distillation (Carleton & Dunham, 2003)) runs out and then it

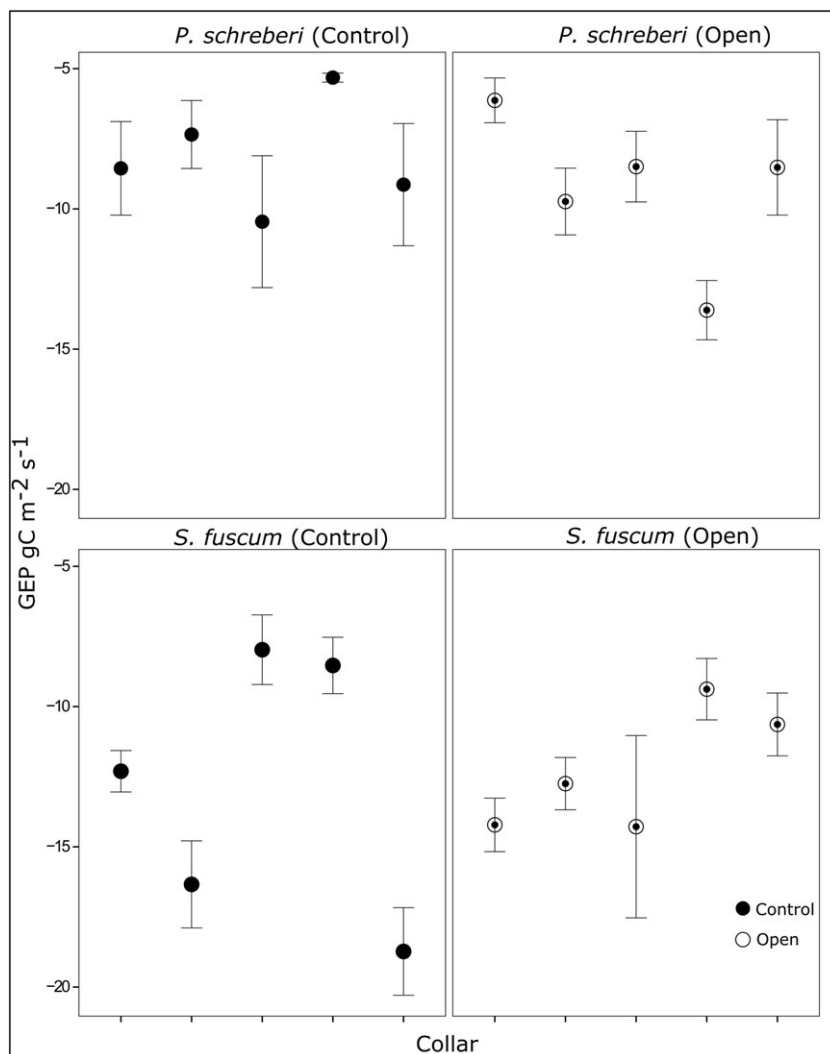


FIGURE 1 Mean (\pm SE) gross ecosystem productivity for each collar ($n = 5$) with five repeat measurements, 2014

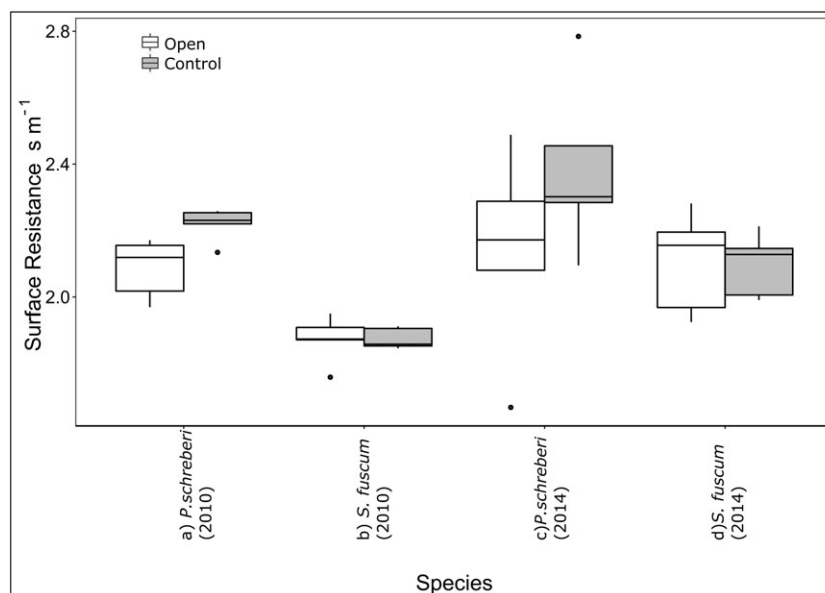


FIGURE 2 Mean (\pm SE) surface resistance of *Pleurozium schreberi* and *Sphagnum fuscum* in open and control plots, 2010 and, 2014 ($n = 5$)

becomes stressed. Surface resistance is a measure of resistance to evaporation from the peat surface: low surface resistance allows high evaporation rates and vice versa. Surface resistance varies with precipitation and is therefore highly variable within a subhumid climate. This is supported by highly variable r_s , GEP, and F_v/F_m measurements for control plots. Evaporative stress is likely happening for a greater proportion of the day and is likely the cause of the long-term decline in *P. schreberi* abundance. There was also no significant change observed in *S. fuscum* r_s and GEP. *S. fuscum* can access water at depth, allowing it

to meet most increases in evaporative demand (e.g., increased energy at the surface) and maintain consistent r_s and GEP rates. This is supported by F_v/F_m values that were consistently near the optimum range in both treatment and control plots (Figure 4). Although no significant changes in r_s and GEP were observed between treatments, significant differences were found between species for GEP and r_s , supporting suggestions that species compositions have the dominant control over C and water fluxes (Heijmans, Arp, & Chapin, 2004). In the short-/medium-term, moss layer hydrology and biogeochemistry have not

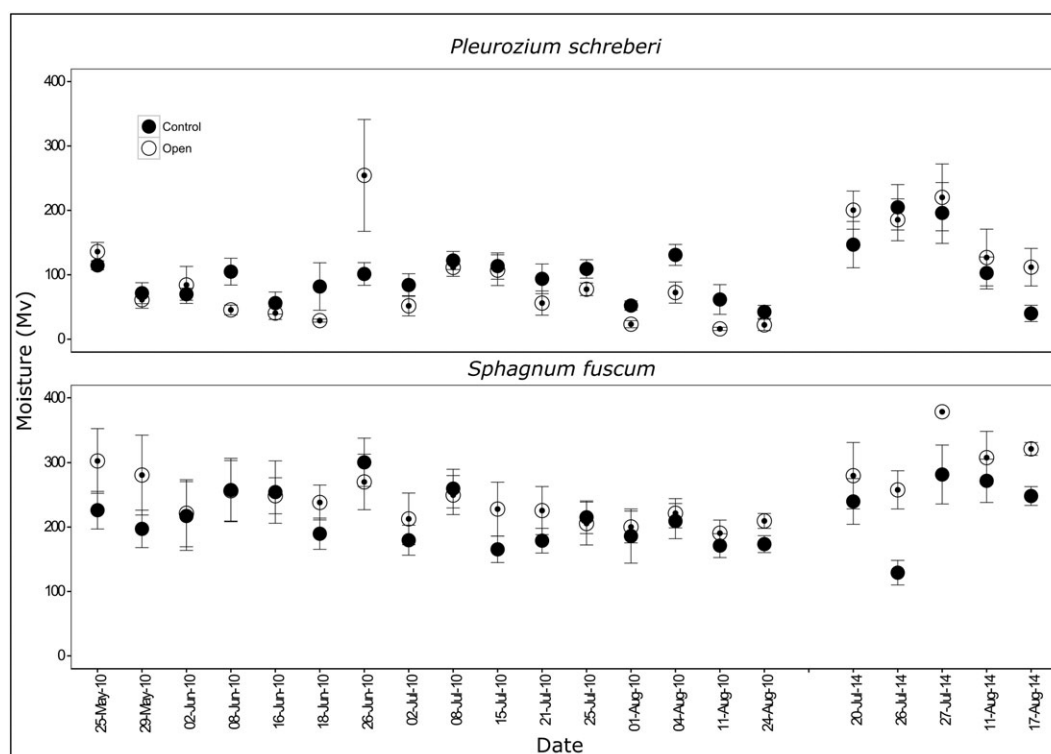


FIGURE 3 Mean (\pm SE) moisture data ($n = 5$) for treatment and control plots of *Pleurozium schreberi* and *Sphagnum fuscum* before and after treatment. (Black spruce canopy was removed on the 17th of June 2010)

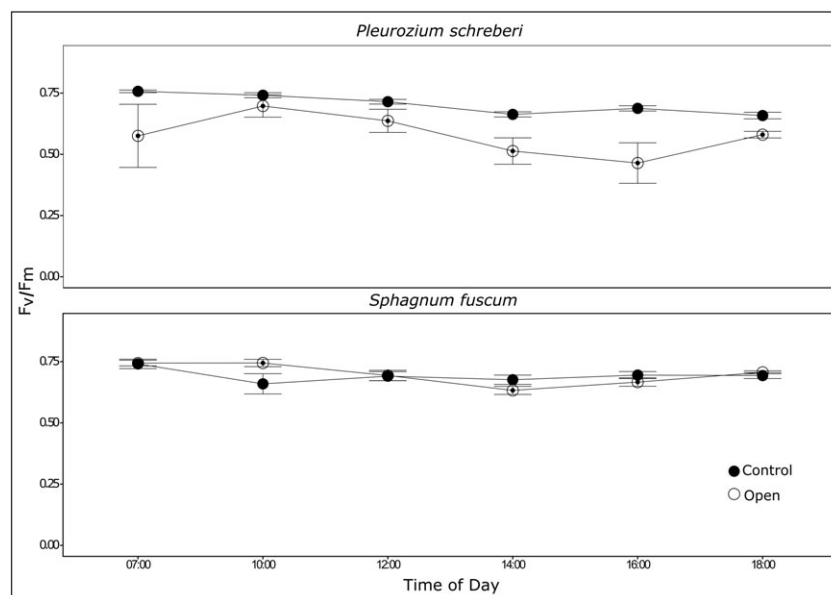


FIGURE 4 Mean (\pm SE) F_v/F_m values for control and treatment *Pleurozium schreberi* (2015), and control and treatment *Sphagnum fuscum* (2015), $n = 5$

changed, suggesting that these peatlands show some degree of resistance to disturbances. The lack of changes in surface resistance and GEP coupled with a decrease in transpiration from the tree-canopy suggests that less water is lost from the ecosystem through evapotranspiration, which facilitates the maintenance of the peatlands' existing, globally important, carbon stock. In the longer term, a shift toward an *S. fuscum* dominated moss layer is suggested by the F_v/F_m data, moss physiology and because feather mosses are characteristic of areas with low light levels (Bisbee et al., 2001). Such a shift in species composition will significantly change the moss layer hydrology and biogeochemistry of moss layers by increasing evapotranspiration and carbon accumulation.

Bryophyte species act a first order control on the small scale atmospheric carbon and water fluxes from peatlands. Ecohydrological feedback models that assume moss layer species change in equilibrium with tree-canopy PAR (BETA model; Kettridge et al., 2013) may provide a poor estimation of water fluxes during any transition period. Although PAR is a distinguishing feature between *P. schreberi* and *S. fuscum* dominated peatlands, the species compositional response to increased PAR is not immediate. This delayed response, compared to immediate responses of the same species within other studies (Shields et al., 2007) highlight that different environmental factors, has varying controls over species competitive strengths and response rates to disturbances. As such, including appropriate disturbance response rates in ecohydrological models could dramatically improve their carbon and water balance prediction capabilities. For example, in this study, we predict a shift toward an *S. fuscum* dominated system and increased carbon accumulation and evaporation from the moss layer, provided trees do not reestablish quickly. However, if the rate at which trees reestablish is faster than the rate at which *P. schreberi* cover significantly declines, the system could revert back to the status quo without significant changes to biogeochemistry and hydrology. Understanding species response rates provides better insight into ecosystem resistance to disturbance, ecohydrological feedback mechanisms, and quantification of carbon and water fluxes within globally important peatland systems.

6 | CONCLUSION

Within the studied peatland, no significant changes in species composition, surface resistance, or carbon fluxes from the bryophyte layer were observed as a result of tree-canopy removal. This study was uniquely conducted in a peatland system where confounding changes associated with tree-canopy clearance (e.g., significant water table changes and machinery influences) were avoided, allowing confident interpretation of results that were a direct effect of tree-canopy removal. These results showed slower changes (40% decrease in *P. schreberi* after 4 years) than those observed in short-term studies undertaken within mineral soils, which suggest that water table variations and/or harvest method may modify the responses of species to tree-canopy removal. Long-term changes are likely to result in a shift toward an *S. fuscum* dominated system as a result of evaporative stress causing weakened competitive strength of *P. schreberi* and eventual mortality. Because species have a dominant control over carbon and water fluxes from the system after tree-canopy removal, we argue that further process-based understanding of moss species compositional change over medium to long-term is essential for more accurate estimations of carbon and water fluxes in these globally important ecosystems.

ACKNOWLEDGMENTS

We would like to acknowledge and thank Laura Bombonato, Dan Thompson, and Steve Baisley for field support and initial set-up of this investigation. Financial support was provided by a Natural Environment Research Council studentship funding, Syncrude Canada Ltd and Canadian Natural Resources Ltd (SCL4600100599 to K. J. D., R. M. P., C. A. M., N. K., and J. M. W.) and Natural Sciences and Engineering Research Council (NSERC-CRD CRDPJ477235-14 to K. J. D., R. M. P., C. A. M., and J. M. W.).

REFERENCES

Adams, W. W., & Demmig-Adams, B. (2004). Chlorophyll fluorescence as a tool to monitor plant response to the environment. In G. C.

- Papageorgiou, & Govindjee (Eds.), *Chlorophyll a fluorescence—A signature of photosynthesis*. 583–604. Netherlands: Springer.
- Birse, E. M. (2016). Ecological studies on growth-form in bryophytes : III. The relationship between the growth-form of mosses and ground-water supply. *Journal of Ecology*, 46(1), 9–27. doi:10.2307/2256900
- Bisbee, K., Gower, S. T., Norman, J. M., & Nordheim, E. V. (2001). Environmental controls on ground cover species composition and productivity in a boreal black spruce forest. *Oecologia*, 129(2), 261–270. doi:10.1007/s004420100719
- Bond-Lamberty, B., Gower, S. T., Amiro, B., & Ewers, B. E. (2011). Measurement and modelling of bryophyte evaporation in a boreal forest chronosequence. *Ecohydrology*, 4(1), 26–35. doi:10.1002/eco.118
- Busby, J. R., Bliss, L. C., & Hamilton, C. D. (1978). Microclimate control of growth rates and habitats of the boreal forest mosses, *Tomenthypnum nitens* and *Hylocomium splendens*. *Ecological Monographs*, 48(2), 95–110. doi:10.2307/2937294
- Carleton, T. J., & Dunham, K. M. M. (2003). Distillation in a boreal mossy forest floor. *Canadian Journal of Forest Research*, 33(4), 663–671. doi:10.1139/x02-197. Retrieved from <http://dx.doi.org/10.1139/x02-197>
- Clymo, R. S., & Duckett, G. (1986). Regeneration of Sphagnum. *New Phytologist*, 102, 589–614. doi:10.1111/j.1469-8137.1986.tb00834.x
- Fenton, N. J., Frego, K. A., & Sims, M. R. (2003). Changes in forest floor bryophyte (moss and liverwort) communities 4 years after forest harvest. *Canadian Journal of Botany*, 81(7), 714–731. doi:10.1139/b03-063
- Fenton, N. J., & Bergeron, Y. (2007). Sphagnum community change after partial harvest in black spruce boreal forests. *Forest Ecology and Management*, 242(1), 24–33. doi:10.1016/j.foreco.2007.01.028
- Heijmans, M. M. P. D., Arp, W. J., & Chapin, F. S. (2004). Carbon dioxide and water vapour exchange from understory species in boreal forest. *Agricultural and Forest Meteorology*, 123(3–4), 135–147. doi:10.1016/j.agrformet.2003.12.006
- Johnson, E. A. (1981). Vegetation organization and dynamics of lichen woodland communities in the Northwest Territories Canada. *Ecology*, 62(1), 200–215. doi:10.2307/1936682
- Kettridge, N., Thompson, D. K., Bombonato, L., Turetsky, M. R., Benscoter, B. W., & Waddington, J. M. (2013). The ecohydrology of forested peatlands: Simulating the effects of tree shading on moss evaporation and species composition. *Journal of Geophysical Research: Biogeosciences*, 118(2), 422–435. doi:10.1002/jgrg.20043
- Locky, D. A., & Bayley, S. E. (2007). Effects of logging in the southern boreal peatlands of Manitoba Canada. *Canadian Journal of Forest Research*, 37(3), 649–661. doi:10.1139/X06-249
- Mariani, L., Chang, S. X., & Kabzems, R. (2006). Effects of tree harvesting forest floor removal and compaction on soil microbial biomass microbial respiration and N availability in a boreal aspen forest in British Columbia. *Soil Biology and Biochemistry*, 38(7), 1734–1744. doi:10.1016/j.soilbio.2005.11.029
- Maxwell, K., & Johnson, G. N. (2000). Chlorophyll fluorescence—a practical guide. *Journal of Experimental Botany*, 51(345), 659–668. doi:10.1093/jexbot/51.345.659
- McCarter, C. P. R., & Price, J. S. (2014). Ecohydrology of Sphagnum moss hummocks: Mechanisms of capitula water supply and simulated effects of evaporation. *Ecohydrology*, 7(1), 33–44. doi:10.1002/eco.1313
- McGuire, D. A., Melillo, J. M., Kicklighter, D. W., & Joyce, L. A. (1995). equilibrium responses of soil carbon to climate change: Empirical and process-based estimates. *Journal of Biogeography*, 22(4/5), 785–796.
- McLeod, M. K., Daniel, H., Faulkner, R., & Murison, R. (2004). Evaluation of an enclosed portable chamber to measure crop and pasture actual evapotranspiration at small scale. *Agricultural Water Management*, 67(1), 15–34. doi:10.1016/j.agwat.2003.12.006
- Pothier, D., Prévost, M., & Auger, I. (2003). Using the shelterwood method to mitigate water table rise after forest harvesting. *Forest Ecology and Management*, 179(1–3), 573–583. doi:10.1016/S0378-1127(02)00530-3
- Raffa, K. F., Aukema, B. H., Bentz, B. J., Carroll, A. L., Hicke, J. A., Turner, M. G., & Romme, W. H. (2008). Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. *BioScience*, 58(6), 501–517. doi:10.1641/b580607
- Shaver, G. R., Street, L. E., Rastetter, E. B., Van Wijk, M. T., & Williams, M. (2007). Functional convergence in regulation of net CO₂ flux in heterogeneous tundra landscapes in Alaska and Sweden. *Journal of Ecology*, 95(4), 802–817. doi:10.1111/j.1365-2745.2007.01259.x
- Shields, J. M., Webster, C. R., & Glime, J. M. (2007). Bryophyte community response to silvicultural opening size in a managed northern hardwood forest. *Forest Ecology and Management*, 252(1–3), 222–229. doi:10.1016/j.foreco.2007.06.048
- Stannard, D. I. (1988). Use of a hemispherical chamber for measurement of evapotranspiration. In *Open-File Report* (pp. 88–452). Denver, CO: United State Geological Survey.
- Timoney, K., & Lee, P. (2001). Environmental management in resource-rich Alberta Canada: first world jurisdiction Third World analogue? *Journal of Environmental Management*, 63(4), 387–405. doi:10.1006/jema.2001.0487
- Wieder, R. K., Scott, K. D., Kamminga, K., Vile, M. A., Vitt, D. H., Bone, T., ... Bhatti, J. S. (2009). Postfire carbon balance in boreal bogs of Alberta, Canada. *Global Change Biology*, 15, 63–81. doi:10.1111/j.1365-2486.2008.01756.x
- Yu, Z. C. (2012). Northern peatland carbon stocks and dynamics: A review. *Biogeosciences*, 9(10), 4071–4085.

How to cite this article: Leonard, R., Kettridge, N., Krause, S., Devito, KJ., Granath, G., Petrone, R., Mendoza, C., Waddington, JM. Peatland bryophyte responses to increased light from black spruce removal. *Ecohydrol.* 2017;10:e1804. doi:10.1002/eco.1804.